A REVISION OF POGONOLEPIS STEETZ (COMPOSITAE: INULEAE: GNAPHALIINAE)

by

P. S. Short*

ABSTRACT

Short, P. S. A revision of *Pogonolepis* Steetz (Compositae: Inuleae: Gnaphaliinae). *Muelleria* 6(4):237-253 (1986). — The endemic Australian genus *Pogonolepis* Steetz is revised. Two species, *P. stricta* Steetz and *P. muelleriana* (Sond.) P. Short, are recognised. They differ from each other in anther dimensions and pollen grain number. Both species exhibit variation in chromosome number. Evolution of the group and taxonomic concepts are discussed. Lectotypes are chosen for the names *P. stricta, Angianthus plumiger* Benth., *A. strictus* (Steetz) Benth. var. *lanigerus* Ewart & J. White and *Skirrophorus muellerianus* Sond.

INTRODUCTION

The genus *Pogonolepis* Steetz has been reinstated following a revision of *Angianthus* Wendl. s. lat. (Short, 1983). It is readily distinguished from other segregate genera of *Angianthus* s. lat. by both the capitular bracts and the inner bracts of the general involucre which are papillate about the apex (these are the 'bearded scales' to which the generic name alludes) and by the fruit morphology.

In the above-mentioned revision I drew attention to the fact that although the genus was distinct it consisted of a number of somewhat ill-defined, closely related taxa which, as indicated by pollen-ovule ratios, exhibited different breeding systems and an array of chromosome numbers (n = 4, 5, 6, 7, c. 10, c. 12). In the present study additional determinations of pollen-ovule ratios and chromosome numbers suggest that a number of biological species exist within the genus. However it is felt that only two morphological species can be recognised.

MATERIALS AND METHODS

Descriptions of taxa were made from dried herbarium material and from specimens stored in 70% ethanol. Shapes were defined using the terms given by the Systematics Association Committee for Descriptive Terminology (1962).

Specimens were examined from the following herbaria: AD, BRI, CANB, CBG, K, KP (Kings Park, Western Australia), MEL, NSW, NT, PERTH, S and UWA (abbreviations after Holmgren & Keuken 1974). Much material was also obtained during field trips to Western Australia in 1977, 1979, 1982 and 1983 and during field work in South Australia and Victoria.

POLLEN-OVULE RATIOS AND ANTHER DIMENSIONS

Only bisexual florets, each with a single ovule, occur in *Pogonolepis* and thus to determine pollen-ovule ratios (henceforth abbreviated as P/Os) it was only necessary to ascertain the number of pollen grains per floret. P/Os were determined on a population basis, the number of pollen grains being determined for at least 15 florets, sampled from different plants.

Measurements pertaining to anther characteristics, i.e. total length, length of the microsporangium and length of the terminal anther appendage, were also determined on a population basis. The anther tails were not included in measurements.

---

* National Herbarium of Victoria, Birdwood Avenue, South Yarra, Victoria, Australia 3141.

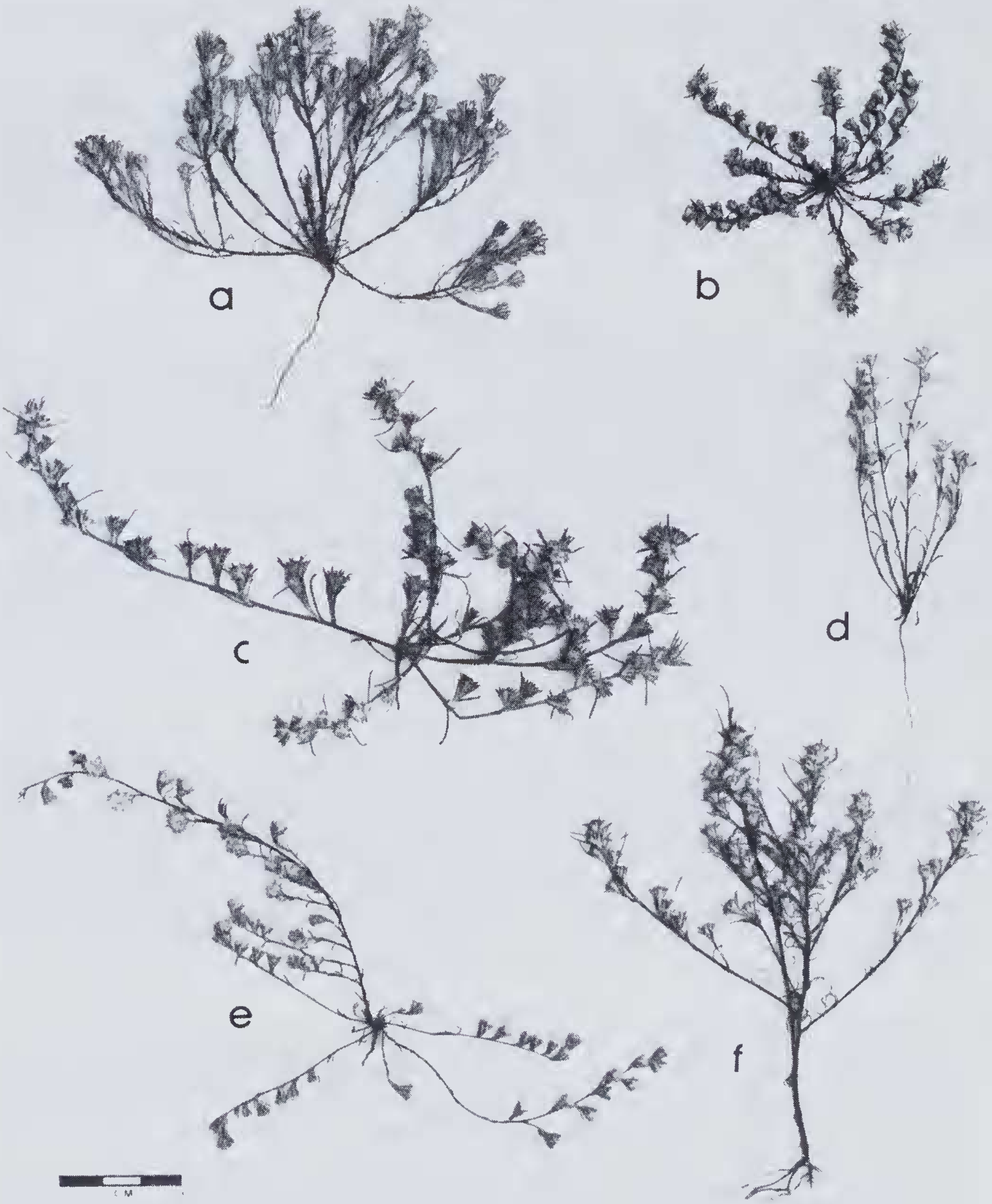

Fig. 1. Specimens of *Pogonolepis*. a — *P. muelleriana (Chinnock 2115)*. b — *P. muelleriana (Chinnock 4357)*. c — *P. stricta (Short 1551)*. d — *P. stricta (Short 2201)*. e — *P. stricta (Short 1513)*. f — *P. stricta (Short 1053)*.

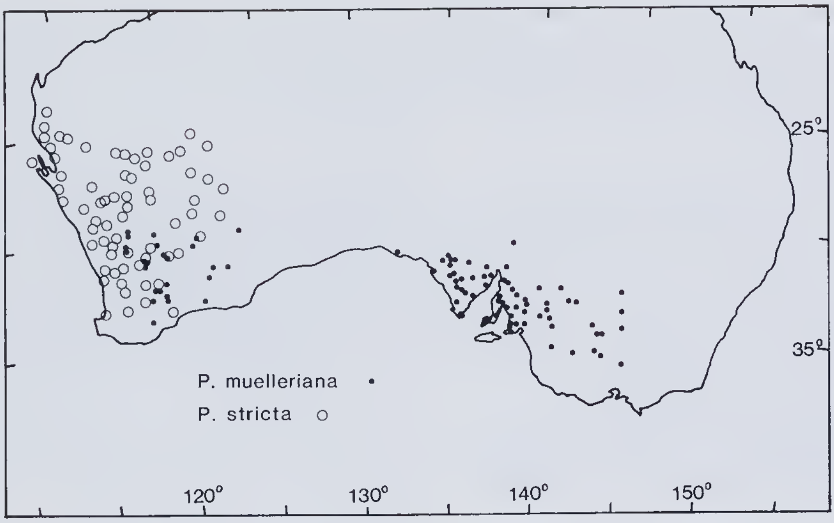

Fig. 2. Distribution of species of *Pogonolepis*.

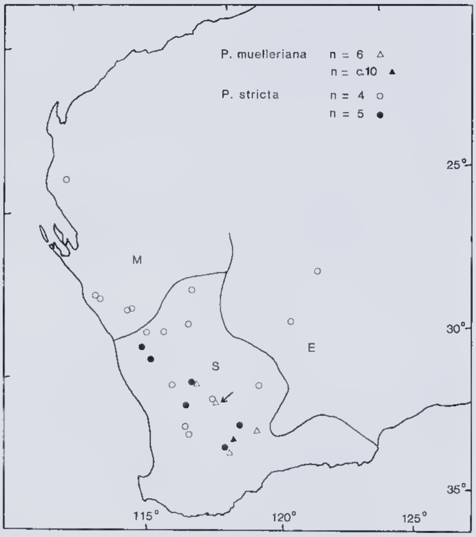

Fig. 3. Distribution of populations of *Pogonolepis* of known chromosome number. Major Drainage Divisions are marked: E = Eucla Division; M = Murchison Division; S = South West Division. The arrow indicates population *Short 648* (2n = 12 + 2 Bs).

As far as possible anther measurements and P/Os have been ascertained for populations for which chromosome numbers have been determined. In some cases this has meant that the same populations have been sampled at different times and are represented by different collector's numbers, e.g. *Short 960 & Short 2219* represent the same population.

PERCENTAGE FRUIT SET

Sixteen populations, eight with high P/Os and eight with low P/Os (see Table 4) were examined for fruit set. Twenty plants were examined in each population and the percentage fruit set was determined for a single, mature, compound head from each plant. Mature fruits are swollen and therefore readily discernible; undeveloped fruits are shrivelled.

Seed viability has not been stringently tested. However the percentage germination of seeds at room temperature and under normal daylight conditions was often high (to c. 80%). Thus the visual method of determining the presence of mature, viable fruit was considered to be reliable.

CYTOLOGY

Cytological material was obtained from either floral buds fixed in the field or from root tips obtained from freshly germinated seed. The floral material was fixed in a solution of 4 parts chloroform, 3 parts absolute ethanol and 1 part glacial acetic acid and the chromosome counts determined from dividing pollen mother cells stained with aceto-carmine. Root tips were pretreated in a 20 ppm solution of o-isopropyl-N-phenylcarbamate (Storey & Mann 1967) for 2-3 hours. They were then fixed in a solution of 3 parts absolute ethanol and 1 part glacial acetic acid for 20 minutes, hydrolised in 1N HC1 at room temperature for 10 minutes, then squashed in aceto-orcein stain.

Successful chromosome preparations have been photographed and the photographic negatives have been placed with the respective voucher collections which are housed in either AD or MEL.

RESULTS AND DISCUSSION

MORPHOLOGY AND SPECIES CONCEPTS

In a previous publication (Short 1981) I suggested that perhaps six morphologically distinct taxa existed in *Pogonolepis.* It seemed that three or four taxa, all with high P/O values, and at least two taxa, each with low P/O values, would ultimately be distinguished. Apart from differences in P/O value it was felt that differences in habit (stem distinct or indistinct; major axes prostrate, decumbent, ascending or erect), leaf density (number per unit length of major axes), relative lengths of the leaves and the minor axes and vestiture and number of leaf-like bracts in the general involucre were a means by which a number of taxa could be recognised. Some of the variation exhibited within the genus is displayed in Fig. 1. As a result of this initial sorting I (Short 1981, 1983) formally made the combinations *Pogonolepis muelleriana* (Sond.) P. Short and *Pogonolepis lanigera* (Ewart & White) P. Short.

I have subsequently examined in more detail the morphological variation exhibited by *Pogonolepis* and it is now apparent that only two morphologically distinct species, i.e. *P. muelleriana* and *P. stricta,* can be recognised. Both are primarily distinguished by differences in P/O values and anther characteristics (Tables 1 & 2). The use of such features in distinguishing species has been discussed for the genus *Actinobole* Fenzl ex Endl. (Short 1985).

Macromorphological variation is such that, although there is sometimes an ecological and/or geographical basis to the variation, various combinations of characteristics tend to occur in different populations. This makes the recognition of taxa on macromorphological grounds untenable. Nonetheless some features can be a useful guide to the identification of species. Thus the majority of collections of *P. muelleriana* are not dissimilar to the specimen shown in Fig. 1a. This specimen is characterised by the apparently large number of leaf-like bracts of the general involucre and by having the leaves quite densely distributed along the major axes. However, particularly in Western Australia, there are specimens (e.g. *Chinnock 4357,* Fig. 1b) which display somewhat different macromorphological features and at times more or less resemble entities of *P. stricta,* so much so that I have not been able to find quantifiable, macromorphological differences between the species.

On the few occasions that I have found both species in the same locality they have tended to exhibit different ecological preferences (e.g. see Table 2, *Short 960 & Short 963*) although there has always been some intermixing. Most importantly, specimens of possible hybrid origin have not been detected.

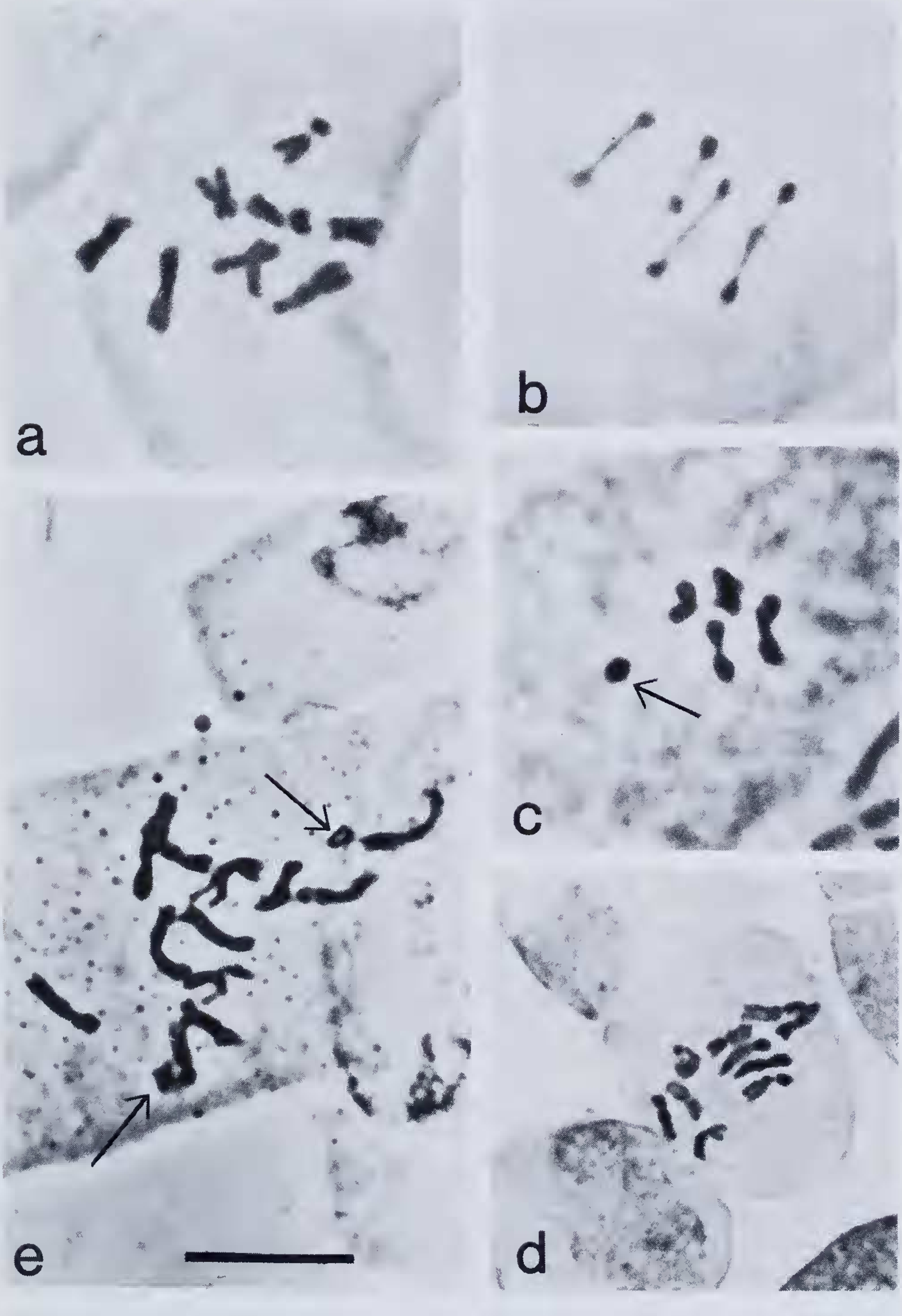

Fig. 4. Chromosomes in *Pogonolepis*. *P. stricta* a — d. a — 2n = 8 *(Short 534.)* b — n = 4 *(Short 1633).* c — n = 4 + 1B *(Short 1551). d — 2n = 10 (Short 1017). P. muelleriana* e — 2n = 12 + 2Bs *(Short 648.)* B chromosomes are indicated by arrows. All figures at same magnification. Scale: 10 μm.

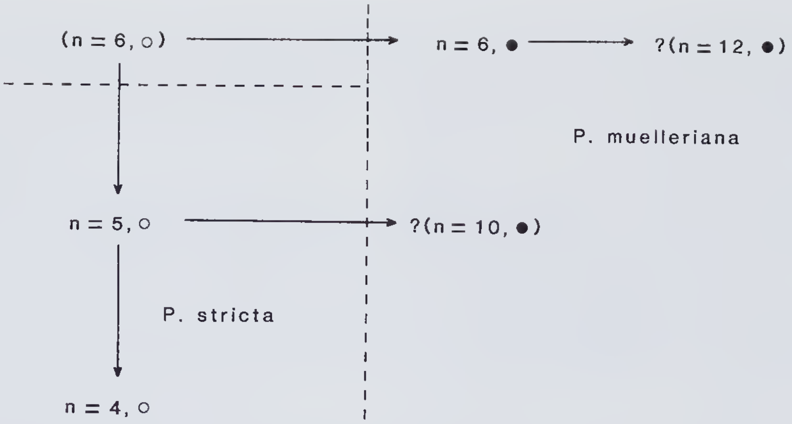

Fig. 5. Evolution in *Pogonolepis*. ( ) = hypothetical taxon. ?( ) = unsubstantiated or likely chromosome number. ○ = outcrosser. ● = selfer.

Table 1. P/Os and anther characteristics of *Pogonolepis*.

Characteristic	Species	x̄	S.D.	S.E.x̄	Range	n	Populations
Pollen grains per floret (P/O)	P. stricta	3,246.0	541.7	62.5	2,000-4,260	75	5
	P. muelleriana	239.3	65.0	5.3	62-404	150	9
Total anther length (mm)	P. stricta	1.04	0.01	0.001	0.85-1.3	90	6
	P. muelleriana	0.58	0.06	0.004	0.38-0.8	195	12
Length of microsporangia (mm)	P. stricta	0.83	0.09	0.01	0.65-1.07	90	6
	P. muelleriana	0.34	0.06	0.004	0.17-0.49	195	12
Length of terminal anther appendage (mm)	P. stricta	0.21	0.04	0.004	0.12-0.34	90	6
	P. muelleriana	0.24	0.05	0.003	0.10-0.48	195	12

In accepting a morphological species concept, there is the inherent problem that such species may not equate well with biological species. Thus from the cytological data (Tables 2 & 3) it is evident that both *P. muelleriana* and *P. stricta* are composed of two or more cytotypes. Furthermore, if the cytological data and the proposed cytoevolutionary pathway (Fig. 5) are correct, then at least *P. muelleriana* is polyphyletic.

POLLEN/OVULE RATIOS, BREEDING SYSTEMS AND FRUIT SET

The most detailed observations on breeding systems within the Australian Compositae have been made by Lawrence (1985) in *Senecio* L.. This work involved both the bagging and cross-pollination of individuals to ascertain self-compatibility, and the determination of P/Os. Not surprisingly there was a strong correlation of breeding system with P/Os, self-incompatible species having high P/Os (2315-7008) and self-compatible species low P/Os (43-237). The usefulness of P/Os has been documented by a number of other workers (e.g. Cruden 1977; Webb 1984) and I have also used P/Os to infer differences in breeding systems between related species of Australian Inuleae (Short 1981, 1983, 1985). In one paper (Short 1981) I noted that differences in P/Os existed between taxa of *Pogonolepis*. These preliminary observations are now confirmed.

Table 2. Chromosome numbers in *Pogonolepis*.

Collection	Chromosome Number		
	n	2n	No. of individuals
Pogonolepis stricta			
Short 960 Saline depression c. 29.5 km N. of Wyalkatchem. Next to Cowcowing cemetery. 30°58'S, 117°27'E. Growing in sandy loam or loam with *Halosarcia & Carpobrotus* and extending into *Atriplex* zone. 14.xi.1979 (AD).		10	8
Short 1009 Eastern edge of Yarra Yarra Lake c. 12 km N. of Carnamah. 29°38'S, 115°50'E. In open areas between *Acacia* shrubs c. 10 m above *Haloscarcia* zone. 19.xi.1979 (AD).		10	4
Short 1017 Salt lake c. 54.5 km from Nugadong toward Gunyidi. 30°07'S, 116°11'E. Upper edge of *Halosarcia* zone and amongst *Melaleuca*. 19.xi.1979 (AD).		10	3
Short 1039 c. 3.5 km E. of Meckering in Mortlock R. flats. 31°37'S, 117°02'E. Amongst *Halosarcia, Acacia,* 20.xi.1979 (AD).		10	2
Short 1083 c. 8.6 km W. of Lake Grace on Kukerin road. Lake Grace (North Lake). 33°06'S, 118°22'E. Growing amongst *Halosarcia* and *Atriplex*. 24.xi.1979 (AD).		10	5
Short 1090 Saline depression c. 10.6 km from Hyden along road to Lake Varley. 32°28'S, 118°57'E. Amongst *Halosarcia* and *Melaleuca*. 25.xi.1979 (AD).		10	1
Short 1551 1 km N. of Boologooro Homestead along NW. coastal highway. 24°20'S, 114°02'E. Sand plain. In open areas between shrubs of *Eremophila, Hakea, Acacia* and chenopods. 25.viii.1982 (AD, CANB, MEL, NSW, PERTH).	4 + 1B (seen at MI & AI)		2
Short 372 13 km from Pindar on road to Mullewa. 28°31'S, 115°41'E. Loam. 16.viii.1977 (AD).	4		1
Short 534 15.3 km S. of Mt. Magnet on Paynes Find road. 28°12'S, 117°52'E. Sandy loam. *Acacia* sp. dominant. 17.ix.1977 (AD).		8	2
Short 928 Edge of saline depression 4.7 km E. of Yellowdine. 31°17'S, 119°42'E. Extending from the upper edge of *Halosarcia* zone to *Melaleuca/Eucalyptus* zone. Sandy loam. 13.xi.1979 (AD).		8	3
Short 988 & 1614 Saline depression 34.5 km N. of Perenjori along road to Morawa. 29°16'S, 116°01'E. Sand to sandy loam. Amongst *Halosarcia*. 15.xi.1979 (AD), 3.ix.1982 (MEL).	4	8	5
Short 995 10 km W. of Pindar. 28°31'S, 115°43'E. Salt lake. In upper *Halosarcia* zone and *Melaleuca* zone on sand. 15.xi.1979 (AD).		8	1
Short 998 2.5 km S. of Binnu. 28°03'S, 114°40'E. Salt flats. Amongst *Halosarcia* and extending into *Melaleuca, Acacia* scrub. 16.xi.1979 (AD).		8	4
Short 1036 8 km W. of Kalguddering. 30°59'S, 116°41'E. Saline depression in Mortlock River (North Branch). Amongst *Halosarcia* 20.xi.1979 (AD).		8	5
Short 1047 16 km from Brookton along road to Beverley. 32°14'S, 116°59'E. In sandy loam between *Acacia* shrubs in ± fresh to semi-saline depression. 21.xi.1979 (AD).		8	2
Short 1050 Hotham R. crossing 7.2 km N. of Popanyinning. 32°36'S, 117°06'E. Between samphire and *Carpobrotus*. 21.xi.1979 (AD, MEL).		8	1
Short 1513 17 km from Menzies along road to Leonora. 29°35'S, 121°08'E. Sand. With chenopod *(Atriplex, Maireana)* and *Eremophila* shrubs. 19.viii.1982 (MEL).	4		1
Short 1538 38 km S. of Bandya Homestead on road to Laverton. 28°01'S, 122°19'E. In sand between shrubs of *Frankenia, Maireana* and *Carpobrotus*. 21.viii.1982 (MEL).	4		1
Short 1596 1.5 km W. of Ajana. 27°57'S, 114°37'E. *Acacia* scrub, gravel loam. 31.viii.1982 (MEL).	4		2
Short 1601 15.5 km W. of Mullewa along road to Geraldton. 28°36'S, 115°25'E. Mallee eucalypt — *Acacia* scrub. Loam. 1.ix.1982 (MEL).	4		1
Short 1618 4.5 km from Great Northern Highway along road to Fields Find. 29°13'S, 117°40'E. Growing in coarse sandy loam of depression in granite outcrop. 2.ix.1982 (MEL).	4		1

Table 2. Continued.

Collection	Chromosome Number n	2n	No. of individuals
Short 1633 Edge of Mongers Lake. 29°32'S, 116°41'E. In sandy loam amongst samphire. 3.ix.1982 (MEL).	4		1
Short 1643 Saline depression 5 km S. of Morawa along road to Perenjori. 29°15'S, 116°02'E. In compact sand and sandy loam. Amongst low shrubs of *Halosarcia* and *Atriplex*. 3.ix.1982 (MEL).	4		6
Short 1740 Salt flat on E. edge of Hines Hill. 31°33'S, 118°04'E. In sand in open areas between *Atriplex* shrubs and *Carpobrotus*. 17.ix.1982 (MEL).		8	1
Short 1754 4.7 km E. of Yellowdine. 31°17'S, 119°42'E. Edge of saline depression. In sand. Amongst samphire and *Carpobrotus*. 18.ix.1982 (MEL).	4		1
Pogonolepis muelleriana			
Western Australia			
Chinnock 4357 Eclipse Lake. 32°57'S, 118°50'E. On upper reaches of lake on sandy clay. 11.xi.1978 (AD).		c. 20	1
Short 648 13.8 km S. of Merredin. 31°33'S, 118°12'E. *Eucalyptus* woodland. Sandy loam. 22.ix.1977 (AD).		12 + 2Bs	1
Short 1076 25 km N. of Pingrup. 33°18'S, 118°28'E. Amongst *Melaleuca* on sand ridge in salt lake. 24.xi.1979 (AD).		12	1
Short 1093A Southern edge of Lake Varley. 32°42'S, 119°21'E. In sand or sandy loam amongst *Halosarcia, Melaleuca* and *Carpobrotus*. 25.xi.1979 (AD).		12	2
Short 963 c. 29.5 km N. of Wyalkatchem. Next to Cowcowing cemetery. 30°58'S, 117°27'E. In *Atriplex* association above saline depression. Loam. 14.xi.1979 (AD).		12	3
South Australia			
Short 828 6 km SW. of Pt Julia. 34°42'S, 137°49'E. Mallee scrub. Calcareous, sandy brown loam. 26.x.1978 (AD).		c. 24	2

Table 3. Chromosome number, P/O and anther length in populations of *P. muelleriana* and *P. stricta.*

Species	Population	Chromosome number		Pollen grains per floret (P/Os)			Total Anther Length (mm)		
		n	2n	x	S.E.	S.E.	x	S.D.	S.E.
P. stricta	*Short 1053*	—	—	3,185.4	397.7	102.6	1.16	0.099	0.025
	Short 1083	—	10	—	—	—	0.98	0.085	0.015
	Short 960/2219	—	10	3,091.5	523.8	135.2	1.02	0.073	0.019
	Short 1551	4 + 1B	—	2,968.2	532.1	137.3	1.1	0.092	0.023
	Short 372	4	—	3,761.4	516.7	133.4	1.05	0.098	0.025
	Short 928	—	8	3.223.3	413.5	106.7	0.94	0.062	0.016
P. muelleriana (Western Aust.)	*Short 648 & 1743*	—	12	208.8	52.5	13.5	0.57	0.033	0.008
	Short 1745	—	—	318.4	38.9	10.05	0.59	0.025	0.006
	Short 2287 & Haegi	—	—	217.0	84.8	21.9	0.52	0.037	0.009
	Short 1093A	—	12	—	—	—	0.58	0.056	0.014
	Short 1070	—	—	—	—	—	0.58	0.033	0.008
	Short 1076	—	12	—	—	—	0.55	0.038	0.009
	Short 963 & 1656	—	12	286.0	70.3	18.1	0.63	0.034	0.008
P. muelleriana (Eastern Aust.)	*Short 769*	—	—	226.3	28.6	7.3	0.67	0.062	0.016
	Short 777	—	—	270.8	43.8	11.3	0.59	0.063	0.016
	Short 811	—	—	160.8	43.4	11.2	0.51	0.065	0.016
	Short 821, 828 & 870	—	c. 24	229.9	34.9	6.3	0.59	0.054	0.009
	Short 906	—	—	245.4	53.1	13.7	0.64	0.054	0.007

The evidence presented (Tables 1 & 2) suggests that the *P. stricta* complex is composed of outcrossers, i.e. plants which, although possibly self-compatible, commonly cross-pollinate, whereas the *P. muelleriana* complex contains selfers, i.e. plants which predominantly self-pollinate. In the absence of bagging and cross-pollination experiments such an hypothesis is open to question but these results are comparable with P/O differences between the self-compatible taxa and self-incompatible taxa of *Senecio* examined by Lawrence (1985). The conclusions on breeding systems are also supported by the observations below on the percentage fruit set in each species.

It could be expected that plants which are self- or partially self-incompatible and/or have morphological characteristics that tend to prevent self-pollination would have a lower percentage fruit set than related self-compatible, self-pollinating species, i.e. species with high P/Os (e.g. 3,000) are likely to set on average a lower percentage of fruit than species with low P/Os (e.g. 200). Percentage fruit sets were determined for populations representing both the *P. stricta* and *P. muelleriana* complexes (Table 4, Fig. 6). An average percentage fruit set of 68.2% was determined for the *P. stricta* complex compared to 93.3% for the *P. muelleriana* complex. Fruit set in wild populations is likely to be influenced by a number of environmental parameters which are not directly related to the breeding system, e.g. severe frosts or water stress may seriously effect fruit maturation (e.g. Mott 1979). Hence such data must be examined with caution. However the results are such that they strongly support the above hypothesis.

Table 4. Percentage fruit set in populations of *P. muelleriana* and *P. stricta*

Species	Collection	Chromosome Number (n)	Percentage Fruit Set Range	Mean
P. stricta	*Short 960*	5	33.3-92.3	71.9
,,	*Short 1009*	5	51.5-100	76.7
,,	*Short 1090*	5	13.5-94.1	65.7
,,	*Short 928*	4	0.0-96.8	54.7
,,	*Short 995*	4	45.0-100	74.9
,,	*Short 998*	4	37.7-97.3	75.4
,,	*Short 1050*	4	30.0-78.3	58.1
,,	*Short 2034*	4	30.3-93.5	68.2
			Mean for species:	68.2
P. muelleriana	*Short 963*	6	83.3-100	95.0
,,	*Short 1076*	6	84.2-100	95.7
,,	*Short 1093A*	6	80.0-100	92.3
,,	*Short 1096*	—	51.9-100	92.1
,,	*Short 1097*	—	85.7-100	97.7
,,	*Short 2384*	—	76.5-100	91.5
,,	*Short 1070*	—	70.0-100	90.0
,,	*Short 828*	c. 12	68.4-100	92.6
			Mean for species:	93.3

The high percentage fruit sets in *P. muelleriana* require further comment. Over one half of the individuals examined had 95-100% fruit set and in the population *Short 1097* 100% fruit set was recorded in 13 of the 20 individuals examined. The lowest percentage fruit set recorded for an individual in this population was 85.7% (21 florets, 18 with mature fruit). Such high figures suggest that in this species, or some populations of the species, the possibility of apomixis should be considered. However there is no additional evidence to support this suggestion. Apomicts frequently show signs of reduced pollen fertility and/or the morphological variation is such that localised 'microspecies', such as in *Taraxacum* Weber, are discernible.

In *Pogonolepis* pollen formation appears to be quite normal. Thus, in the populations for which P/Os were ascertained, pollen size was not noticeably variable and percentage pollen fertility, determined by the double-stain technique (methyl green and phloxine: Owcarzac 1952) was, or was very close to, 100%. The macromorphological variation in *P. muelleriana,* particularly if one excludes a few of the Western Australian collections, is also inconsistent with the concept of 'microspecies'.

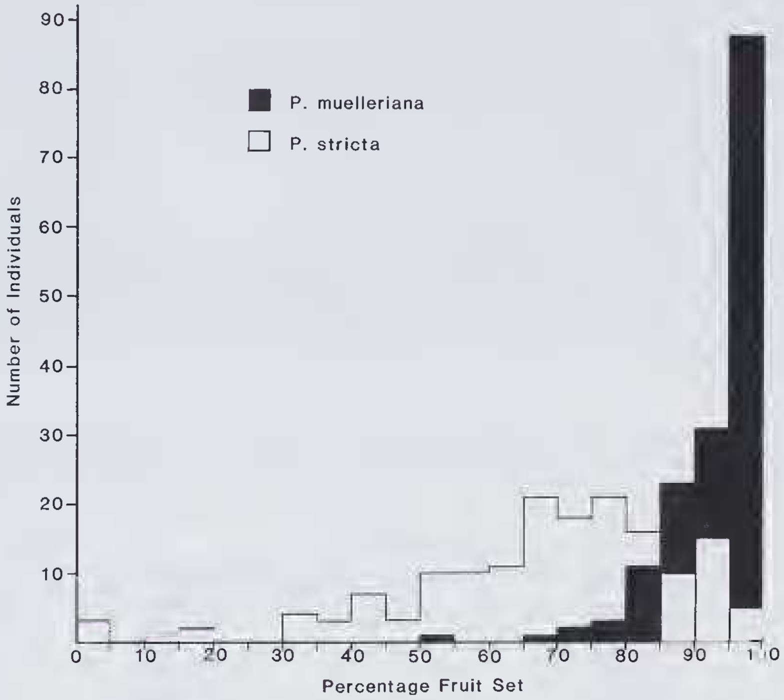

Fig. 6. Percentage fruit set in *Pogonolepis.*

CYTOLOGY

I previously reported (Short 1981) a determination of n = 6 for an outbreeding entity of *Pogonolepis* but I now believe that this determination should be disregarded. There is no permanent slide, sketch or photograph to substantiate it and n = 6 has not been recorded subsequently in *P. stricta.* Similarly a determination of 2n = 14, previously reported as n = 7 (Short 1983), for an inbreeding entity *(Short 648)* is now regarded as 2n = 12 + 2 supernumerary chromosomes (Fig. 4e).

Chromosome numbers were generally readily determined for *P. stricta* from both floral material and root tips. On the other hand, despite numerous attempts, the low number of pollen mother cells produced by members of the *P. muelleriana* complex prevented successful determinations from meiotic material. This is unfortunate as there were some difficulties in accurately determining chromosome numbers from root tip preparations. Thus unequivocal determinations have not been achieved for two collections of *P. muelleriana,* i.e. *Short 828* (2n = c. 24) and *Chinnock 4357* (2n = c. 20). However, the determination of 2n = 24 is strongly supported given the substantiated reports of 2n = 12. Autogamous species are commonly found to consist of both diploid and higher ploid representatives. The determination of 2n = c. 20 should probably be discounted, having been obtained from a single preparation and because n = 5 has not been recorded in *P. muelleriana.* On the other hand there is little doubt that inbreeding is generally a derived condition, the evolution of autogamous taxa (low P/Os) from predominantly outcrossing taxa (high P/Os) being well documented in many families (e.g. Stebbins 1957, Ornduff 1969, Short 1981). Derived, autogamous taxa are also frequently polyploids. This suggests that the collection *Chinnock 4357* could be regarded as a tetraploid, having been derived from an outcrossing entity with a base of x = 5. Such an hypothesis could explain the above-mentioned similarity, on macromorphological features, of this collection with some entities of *P. stricta.*

In any genus showing an array of chromosome numbers it can, in the absence of other information, be difficult to explain their derivation. In *Pogonolepis* the presence of autogamous taxa greatly assists the problem and a proposed phylogeny is displayed in Fig. 5. Thus aneuploid reduction, plus subsequent polyploidy, from a base of x = 6 is suggested.

The cytoevolutionary pathway proposed for *Pogonolepis* has numerous parallels within the Compositae. For example a complete aneupolid reduction series from a base of x =9 to x = 2 has been recorded in *Brachyscome* Cass. (Smith-White *et al.* 1970). In *Calotis* R.Br. Stace (1978) recorded reduction from x = 8 to x = 4 and polploidy was also found to occur on all base numbers. Both of these genera, which are restricted to Australasia, belong to the Astereae. However from my own unpublished observations and from chromosome numbers determined by Turner (1970) it is clear that aneuploidy is widespread in the Gnaphaliinae.

Chromosome Numbers and Distribution Patterns

Without taking into account ecological and geographical differences the distribution of populations with different chromosome numbers, i.e. n = 4 and n = 5, within the *P. stricta* complex displays no obvious pattern other than the fact that the latter populations are more restricted in their distribution than populations with n = 4. However, in keeping with their wide distribution, populations with n = 4 are found in a broad spectrum of habitats (see Table 2). This contrasts with populations with n = 5 which are restricted to salt lakes, all of which form part of the South West Drainage Division (Mulcahy & Bettenay 1972; Bettenay & Mulcahy 1972; Beard 1973). The former populations are distributed across three Drainage Divisions, i.e. the South West, Murchison and Eucla Divisions.

Populations belonging to the *P. muelleriana* complex also occur in an array of habitats, including saline soils, and I believe it significant that different cytoptypes (ie. 2n = 12, 12 + 2B, c. 20) are, as with populations of *P. stricta,* found around lakes of the South West Drainage Division. These observations add further support to my earlier contention (Short 1983) that the lake systems of south-west Western Australia have been reservoirs for speciation and that, for some plant groups, they may have been important reservoirs from which colonization of the arid zone has occurred.

Only a single chromosome number determination has been made for the *P. muelleriana* complex outside Western Australia. The occurrence of a tetraploid population in South Australia may reflect a wider distribution of polyploids compared to the diploid relatives, a not uncommon situation in many plants, but clearly more determinations are required to support this suggestion.

Fruit Morphology and Anatomy

A survey of the fruit morphology and anatomy of Australian Gnaphaliinae has shown that fruit characteristics are most useful when determining generic limits. The absence or presence and type of mucilagenous cells, the structure of the carpophore, the number of vascular bundles and the presence (in medial transverse section) or absence of sclerenchyma are some features which may vary from genus to genus. Thus within *Angianthus* s. lat. only the segregate genera *Pogonolepis* and *Cephalosorus* A. Gray, both distinguishable on numerous non-carpological features (Short 1983), have large, mucilagenous cells covering much of the entire

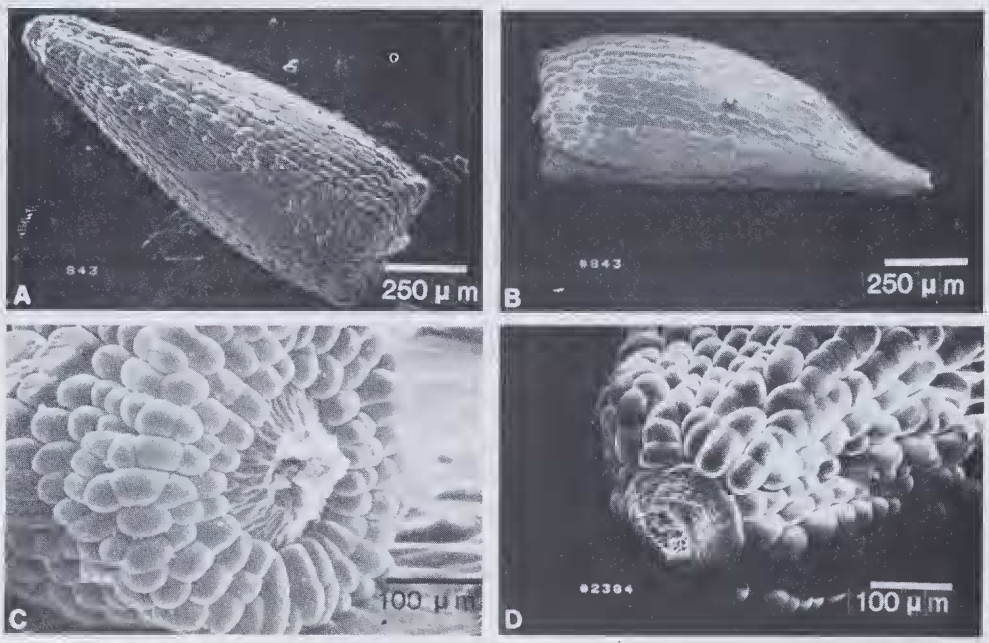

Fig. 7. Surface features of the fruit of *Pogonolepis,* as typified by *P. muelleriana (Short 843; Short 2384 & Haegi).* a & b — general view of entire fruit. c — apex of fruit. d — carpophore.

surface of the fruit (Fig. 7). More details of the fruit structure of *Angianthus* s. lat. will be presented, along with methodology, in a future paper.

As shown in Figs 7a & 7b fruit shape can vary slightly depending on the number of fruits and the position occupied on the general receptacle. Also of note in *Pogonolepis* is the presence of a well-defined carpophore (Fig. 7d), a feature lacking in some genera of Gnaphaliinae.

TAXONOMY

Pogonolepis Steetz in Lehm. Pl. Preiss. 1:440 (1845); P. Short, Muelleria 4:404 (1981); Grieve, W. Aust. Wildfls Suppl 4:72 (1982); P. Short, Muelleria 5:203 (1983). — *Skirrophorus* DC. in Lindl. ex DC. sect. *Pogonolepis* (Steetz) A. Gray, Hook. J. Bot. Kew Gard. Misc. 3:149 (1851); Sond., Linnaea 25:486 (1853). Type: *Pogonolepis stricta* Steetz

[*Angianthus* auct. non Wendl.: as to *A. strictus* (Steetz) Benth. & *A. lanigerus* Ewart & J. White]

[*Siloxerus* auct. non Labill.: as to *S. strictus* (Steetz) Ostenf.]

[*Skirrophorus* auct. non DC. in Lindl. ex DC.: as to *S. strictus* (Steetz) A. Gray & *S. muellerianus* Sond.]

[*Styloncerus* auct. non Spreng., nom. illeg.: as to *S. strictus* (Steetz) Kuntze]

Annual herbs. Major axes decumbent, ascending or erect, variably hairy; stem simple or forming major branches at basal and/or upper nodes. *Leaves* usually alternate (sometimes opposite), sessile, entire, glabrous or sparsely hairy, mucronate. *Compound heads* ± broadly obovoid; bracts subtending compound heads forming a conspicuous, multi-seriate involucre equal to or slightly longer than the length of the head, the outer bracts leaf-like, the inner ones primarily hyaline and with papillae at the apex; *general receptacle* a flat or ± concave, entire, glabrous axis. *Capitula* c. 5-40 per compound head. *Capitular bracts* 2-3, about the length of the florets, ± hyaline, whitish, the midrib ± inconspicuous, the bract apices papillose.

Florets 1 per capitulum, bisexual; corolla tubular, 5-merous, yellow. *Style* branches truncate, with short sweeping hairs, a distinct stylopodium present. *Stamens* 5; anthers with a sterile, deltate to ± triangular, apical appendage; microsporangia tailed, endothecial tissue polarized; filament collar ± straight in outline and composed of ± uniform cells and basally not or barely thicker than the filament. *Cypselae* ± obovoid, covered in mucilagenous cells, with 2 vascular bundles and a distinct carpophore. *Pappus* absent. Figs 1, 7.

Chromosome number: n = 4, 5, 6, c. 10, c. 12 (Fig. 4).

DISTRIBUTION (Figs 2 & 3):

Both species recognised are found in Western Australia but *P. muelleriana* extends to South Australia, New South Wales and Victoria.

KEY TO THE SPECIES OF POGONOLEPIS

1. Anthers 0.85-1.3 mm long; pollen grains 2,002-4,260 per floret and c. 400-850 per anther (Western Australia) .... 1. *P. stricta*

1. Anthers 0.38-0.8 mm long; pollen grains 62-404 per floret and 16-76 per anther (Western Australia and Eastern Australia) .... 2. *P. muelleriana*

1. **Pogonolepis stricta** Steetz in Lehm. Pl. Preiss. 1:440 (1845); P. Short, Muelleria 4:404 (1981); Grieve, W. Aust. Wildfls Suppl. 4:72 (1982); P. Short, Muelleria 5:203 (1983). — *Skirrophorus strictus* (Steetz) A. Gray, Hook. J. Bot. Kew Gard. Misc. 3:149 (1851). — *Angianthus strictus* (Steetz) Benth., Fl. Austr. 3:568 (1867); Grieve & Blackall, W. Aust. Wildfls 816 (1975). — *Styloncerus strictus* (Steetz) Kuntze, Rev. Generum Pl. 367 (1891). — *Siloxerus strictus* (Steetz) Ostenf., Biol. Meddel. Kongel. Danske Vidensk. Selsk. 3:137 (1921). TYPE:"In locis hyeme aqua marina inundatis prope Vasse-Inlet, mense Dec. 1839. Herb. Preiss. No. 39." LECTOTYPE (here designated): *Preiss 39,* In Nova Hollandia, (Swan River Colonia) in locis hyeme inundatis aqua marina, prope Vasse-Inlet leg. cl. Preiss . . . . emi 1843, s.dat. (MEL 541613, ex herb. Steetz). ISOLECTOTYPES: LD, MEL 541612 (ex herb. Sond.), P (2 sheets, one ex herb. Schultz-Bip.), S (herb. Lehm.). POSSIBLE ISOLECTOTYPE: PERTH. See note 1 below.

Angianthus plumiger Benth., Fl. Austr. 3:568 (1867); Grieve & Blackall, W. Aust. Wildfls 816 (1975). TYPE:"Swan and Murchison Rivers, *Oldfield.*" LECTOTYPE (here designated): *Oldfield 82,* Murchison, s.dat. (MEL 84616). REMAINING SYNTYPE: *Oldfield 82,* Swan R., W.A., s.dat. (MEL 84613). See note 2 below.

Angianthus strictus (Steetz) Benth. var. *lanigerus* Ewart & J. White, Proc. Roy. Soc. Vict. 22:92 (1909). — *Angianthus lanigerus* (Ewart & J. White) Ewart & J. White, Proc. Roy. Soc. Vict. 23:288 (1911); Grieve & Blackall, W. Aust. Wildfls 816 (1975). — *Pogonolepis lanigera* (Ewart & J. White) P. Short, Muelleria 5:204 (1983). TYPE: "Woorooloo, West Australia. Max Koch, Oct., 1907. No. 1873." LECTOTYPE (here designated): *Koch 1873,* Woorooloo, -.x.1907 (MEL 541625). ISOLECTOTYPES: NSW (2 sheets), PERTH. See note 3 below.

Annual herb, the major axes prostrate to erect, 2.5-20(26) cm long, ± glabrous to densely hairy in parts, the axes often reddish. *Leaves* narrowly triangular, lanceolate to narrowly lanceolate or ± linear, 4-20(23) mm long, 0.5-1.5 mm wide, glabrous to ± densely hairy, the base ± dilated and the margins often hyaline, the apex barely to prominently mucronate. *Compound heads* 2.7-4.3 mm long, 0.9-4 mm diam., bracts of the general involucre c. 15-25 (c. 35); outer bracts 8-18(27), leaf-like, ± narrowly triangular or lanceolate, 2.8-4 mm long, 0.5-1.1 mm wide, about the length of or exceeding the length of the capitula, sparsely to densely hairy, ± straight to recurved, grading into inner, non-leaf-like bracts; inner bracts 6-13, ± elliptic or ± oblong or ovate or obovate, 2.1-2.7 mm long, 0.6-1 mm wide, with a ± distinct midrib extending from about half to about the full length of the bract, all bracts variably hairy with papillae on the upper part, grading into capitular bracts. *Capitula* (6)15-50(103) per compound head. *Capitular bracts* ±

elliptic or obovate, (1.95)2-2.5 mm long, 0.4-0.6 mm wide, ± flat to conduplicate, the midrib ± indistinct or clearly extending to about three quarters the length of the bract. *Florets* 1 per capitulum; corolla tube 1.5-1.9 mm long. *Anthers* 0.85-1.3 mm long; microsporangia 0.65-1.07 mm long; terminal anther appendage 0.12-0.34 mm long. *Pollen grains* c. 2,000-4,200 per floret, c. 400-850 per anther. *Cypselae* 0.7-0.95 mm long, 0.3-0.45 mm diam. Fig. 1, c-f.

Chromosome numbers: n = 4, 5 (Fig. 4, a-d).

DISTRIBUTION (Figs 2 & 3):

Restricted to Western Australia.

ECOLOGY:

Usually found in sandy soil. Commonly occurs on the edge of saline depressions with *Halosarcia* and other chenopods but also found in open shrubland of *Acacia, Eremophila,* etc. See Table 2 for further details.

NOTES:

1. Steetz described a number of species of Compositae in Lehmann's "Plantae Preissianae" and type specimens of such taxa are frequently found in GH, LD, MEL and S (Short 1983, p.152). It has been suggested that the principal types of all species described in this work are to be found in LD. However it is clear that in the case of taxa described by Steetz this is not, or usually not, the case. The collections from his own herbarium, now at MEL, should undoubtedly be selected as lectotypes (Short l.c.).

A collection *"Preiss 901,* In salsolis hieme aqua inundatis ad aestuary prope Vasse, 14.xii.1839" of *P. stricta* occurs in PERTH (ex TCD, ex K). Despite the different number this collection is probably an isolectotype of *P. stricta*. McGillivray (1975) has noted the existence of a differently numbered set of Preiss specimens in TCD which are undoubted duplicates of those cited in "Plantae Preissianae".

2. The application of the name *Angianthus plumiger* Benth. has previously been in doubt (Short 1983, p.210). Type specimens of this species could not be found at K, BM or E and the reference by Bentham (1867, p.568) to a "flat subtending [bract of the capitulum] which is much shorter than the involucres, but usually with the midrib produced into a jagged almost plumose appendage almost as long as the florets" suggested that the name should not be applied to a species of *Pogonolepis*. Only his reference to the "numerous inner scarious fringed or jagged bracts" of the general involucre suggested this possibility. Whether or not Grieve and Blackall (1975) saw type material is unclear but specimens of *Pogonolepis* were referred to by this name.

I have recently located at MEL undoubted type specimens of *A. plumiger* and they clearly belong to the *P. stricta* complex. Both the lectotype sheet and the remaining syntype contain eight or more plants but in some cases the individual specimens are poorly preserved. At least some individuals have suffered from fungal attack. Bentham's description clearly applied in part to some of the damaged bracts. Bracts of more or less undamaged plants are typical of *Pogonolepis*.

A further Oldfield collection of *Pogonolepis* from the Murchison River housed in MEL (MEL 84622) is not considered to be type material of *A. plumiger* but rather the collection cited by Bentham (l.c.) under *Angianthus strictus*. The label accompanying this specimen carries an unpublished name of Ferdinand Mueller's which commemorates Oldfield.

3. As far as can be ascertained Ewart and White (1909) saw both NSW and MEL material when describing *A. strictus* var. *lanigerus*. The MEL sheet bears several good specimens and also contains the original drawings published by the authors. Furthermore both Ewart and White worked in Melbourne and thus it seems best to select MEL 541625 as the lectotype collection.

Specimens Examined (Total c. 165).

For representative specimens see Tables 2 & 4.

2. **Pogonolepis muelleriana** (Sond.) P. Short, Muelleria 4:413 (1981). — *Skirrhophorus meullerianus* Sond., Linnaea 25:486 (1853). Type: "Inter portum et urbem Adelaide. Spencer's gulph." Lectotype (here designated): *Mueller s.n.,* Inter portum & urbem Adelaide, s.dat. (MEL 541616, ex herb. O.W. Sonder). Possible Isolectotypes: GH (ex herb. O.W. Sonder) (Mueller collection but location given as "Adelaide"), MEL 541614 (ex herb. O.W. Sonder) (Mueller collection but location given as "Adelaide"), MEL 84611 (contains 2 labels, one with ". . . inter portum & urbem Adl. . .", the other with "propa sinum St. Vincent"). Remaining Syntype: MEL 541615 (ex herb. O.W. Sonder) (collection by Mueller from "Spencersgulph"). See note 1 below.

[*Angianthus strictus* auctt. non (Steetz) Benth.: Benth., Fl. Austr. 3:568 (1867), p.p.; J. M. Black, Fl. S. Aust. 1st. ed. 645 (1929), 2nd. ed. 924 (1957); Willis, Handb. Pl. Vict. 2:730 (1973); Grieve & Blackall, W. Aust. Wildfls 816 (1975), p.p.; Cunningham, Mulham, Milthorpe & Leigh, Plants Western N.S.W. 709 (1981).]

Annual herbs, the major axes prostrate to erect, 1-12 cm long, ± glabrous but often densely hairy below the compound heads, all axes ± brown but sometimes distinctly red or reddish brown. *Leaves* narrowly triangular, lanceolate to narrowly lanceolate or ± linear, 3-10(16) mm long, 0.5-1 mm wide, glabrous or sometimes at least the upper ones conspicuously hairy, the base dilated and the margins often hyaline, the apex mucronate, green to purplish green. Compound heads 3.5-4.4 mm long, 2-4.5(4.8) mm diam.; bracts of the general involucre 16-40; outer bracts 7-28(34), leaf-like, ± narrowly triangular or lanceolate, 3.2-4.7 mm long, 0.5-1 mm wide, about the length of or exceeding the length of the capitula, sparsely to densely hairy, ± straight to recurved, green or sometimes purple-green, grading into inner, non-leaf-like bracts; inner bracts 7-20, ± elliptic, ± oblanceolate to obovate, ± oblong or ovate, 2.5-3.4 mm long, 0.6-0.9 mm wide, with a distinct midrib extending about two-thirds the length of the bract, with all bracts variably hairy and with papillae on the upper part. *Capitula* 10-45 per compound head. *Capitular bracts* ± elliptic or obovate, ± flat to conduplicate, 1.9-3.3 mm long, 0.35-0.6 mm wide, midrib ± indistinct or nearly extending to about two-thirds or four-fifths the length of the bract. *Florets* 1 per capitulum; corolla tube 1.55-2 mm long. *Anthers* 0.3-0.8 mm long; microsporangia 0.17-0.49 mm long; terminal anther appendage 0.18-0.48 mm long. Pollen grains 60-404 per floret, (12)20-64(84) per anther. *Cypselae* 0.9-1.2 mm long, 0.3-0.5 mm diam. Fig. 1, a-b.

Chromosome numbers: n = 6, c. 10, c. 12 (Fig. 4e).

Distribution (Figs 2 & 3):

Extends from southern Western Australia to South Australia, New South Wales and Victoria.

Ecology:

Occurs in sand or loam. Extremely common amongst *Halosarcia* and other chenopods on the edge of both coastal and inland saline flats but is also commonly found in a variety of other habitats in which the soil is not saline (see Table 2 for additional data).

Notes:

1. The species was described by Sonder from material sent to him by Mueller. Subsequently it appears that the material was probably returned to MEL when Sonder's collection of Australian plants was purchased by the herbarium (Court 1972). Possibly a number of duplicates exist in other herbaria but it seems reasonable

to choose a lectotype collection from the material held in MEL. The chosen sheet contains two individual plants in good condition, an envelope containing a few bracts and two labels, i.e. *"Pogonolepis Mulleri"* and *"Skirrophorus (Pogonolepis) Muellerianus"*, in Sonder's hand. The collection was also chosen as the lectotype because of the existence of possible isolectotypes. No duplicates of the other syntype have been seen.

SPECIMENS EXAMINED (Total c. 170):
For representative specimens see Tables 2 & 4.

ACKNOWLEDGEMENTS

My work on the Australian Compositae commenced in 1977. Transport and/or funds for field work in Western Australia has been provided by the Botanic Gardens of Adelaide (1977), the Flinders University Research Committee (1979) and Australian Biological Resources Study grants from the Bureau of Flora and Fauna (1982, 1983). The latter body has also funded my survey of the fruit of Australian Gnaphaliinae.

I thank my colleagues at MEL who helped in the preparation of this paper, Dr B. A. Barlow (CANB) for his comments on the manuscript and also Mr J. Nailon of Monash University for the SEM photographs.

REFERENCES

Beard, J. S. (1973). 'The Elucidation of Palaeodrainage Patterns in Western Australia through Vegetation Mapping.' Vegetation Survey of Western Australia, Occasional Paper 1. (Vegmap Publications: Perth).

Bettenay, E. & Mulcahy, M. J. (1972). Soil and landscape studies in Western Australia. (2) Valley form and surface features of the South-West Drainage Division. *J. Geol. Soc. Aust.* 18: 359-369.

Court, A. B. (1972). Preliminary notice on the Sonder collection in the National Herbarium of Victoria. *Muelleria* 2: 188.

Cruden, R. W. (1977). Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32-46.

Holmgren, P. K. & Keuken, W. (1974). 'Index Herbariorum. Part 1. The Herbaria of the World', ed. 1. *Regnum Veg.* 92: 1-397.

Lawrence, M. E. (1985). *Senecio* L. (Asteraceae) in Australia: Reproductive biology of a genus found primarily in unstable environments. *Aust. J. Bot.* 33: 197-208.

McGillivray, D. J. (1975). Johann August Ludwig Preiss (1811-1883) in Western Australia. *Telopea* 1: 1-18.

Mott, J. J. (1979). Flowering, seed formation and dispersal. *In* Goodall, D. W. & Perry, R. A. (eds), 'Arid-land Ecosystems: structure, functioning and management'. (Cambridge Univ. Press). 1: 627-645.

Mulcahy, M. H. & Bettenay, E. (1972). Soil and landscape studies in Western Australia. (1) The major drainage divisions. *J. Geol. Soc. Aust.* 18: 349-357.

Ornduff, R. (1969). Reproductive biology in relation to systematics. *Taxon* 18: 121-133.

Owczarzak, A. (1952). Pollen grains — a rapid method of mounting. *Stain Technol.* 27: 249-253.

Short, P. S. (1981). Pollen-ovule ratios, breeding systems and distribution patterns of some Australian Gnaphaliinae (Compositae: Inuleae). *Muelleria* 4: 395-417.

Short, P. S. (1983). A revision of *Angianthus* Wendl. sensu lato (Compositae: Inuleae: Gnaphaliinae). *Muelleria* 5: 143-214.

Short, P. S. (1985). A revision of *Actinobole* Fenzl ex Endl. (Compositae: Inuleae: Gnaphaliinae). *Muelleria* 6: 9-22.

Smith-White, S., Carter, C. R. & Stace, H. M. (1970). The cytology of *Brachycome* 1. The subgenus *Eubrachycome:* A general survey. *Aust. J. Bot.* 18: 99-125.

Stace, H. M. (1978). Cytoevolution in the Genus *Calotis* R. Br. (Compositae: Astereae). *Aust. J. Bot.* 26: 287-307.

Stebbins, G. L. (1957). Self fertilization and population variability in the higher plants. *Amer. Naturalist* 91: 337-354.

Storey, W. B. & Mann, J. D. (1967). Chromosome contraction by o-isopropyl-N-phenylcarbamate (IPC) *Stain Technol.* 42: 15-18.

Systematics Association Committee for Descriptive Terminology (1962). Terminology of simple symmetrical plane shapes. *Taxon* 11: 145-156, 345-347.

Turner, B. L. (1970). Chromosome numbers in the Compositae. XII. Australian species. *Amer. J. Bot.* 57: 382-389.

Webb, C. J. (1984). Constraints on the evolution of plant breeding systems and their relevance to systematics. *In* Grant, W. F. (ed.), 'Plant Biosystematics'. (Academic Press: Canada). pp. 249-270.

Manuscript received 13 August 1985.